Research Article

The susceptibility of small fruits and cherries to the spotted-wing drosophila, *Drosophila suzukii*

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Abstract

BACKGROUND: The spotted-wing drosophila, *Drosophila suzukii* Matsumura, is native to Asia and was first detected in the North American mainland and Europe in 2008–2010. *Drosophila suzukii* is a serious economic pest to stone and small fruits because the female lays eggs within ripening fruit on a plant before harvest, which can lead to crop loss. The aim of this study was to evaluate the susceptibility of blackberries, blueberries, cherries, grapes, raspberries and strawberries to *D. suzukii* among various ripeness stages and cultivars.

RESULTS: In 26 no-choice and choice replicated laboratory cage tests on ripeness stages, fruits were generally susceptible to *D. suzukii* once fruits started to color. Few *D. suzukii* developed on green fruit, wine grapes or overripe blueberries. In seven cultivar tests, *D. suzukii* preferences ranged from no differences to fourfold differences for specific cultivars of blackberries, blueberries, raspberries and wine grapes. As brix levels increased, more eggs were laid or more *D. suzukii* developed on blackberries, blueberries, cherries, raspberries and strawberries. In a choice test of various fruit types, strawberries, raspberries, blackberries, cherries and blueberries were more susceptible to *D. suzukii* than green table grapes ('Thompson').

CONCLUSION: The results suggest that fruits may become susceptible to *D. suzukii* as they start to turn color, and that specific varieties of grapes and overripe blueberries have low susceptibility to *D. suzukii*.
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Keywords: *Drosophila suzukii*; cultivars; oviposition; ripeness stage

1 INTRODUCTION

The spotted-wing drosophila, *Drosophila suzukii* Matsumura, an invasive vinegar fly from Asia, was detected in ten states of the mainland United States and in British Columbia, Italy, France and Spain in 2008–2010.[1] Similarly to Japanese records, infestations in the United States have been observed on several important crops: blackberries, blueberries, cherries, peaches, raspberries and strawberries. Damage has been considered to range from negligible to 80% crop loss.[2,3] Understanding cultivar preferences and ripeness stages of fruits most susceptible to infestation by *D. suzukii* is needed to improve management practices. This knowledge can lead to selection of more resistant fruits/cultivars and determination of optimal timing of treatments. Limited information on the biology of *D. suzukii* is available, mostly from studies conducted in Japan. In one comparison, 11% of eggs were laid on unripe cherries, 34% on slightly ripe cherries and 55% on fully ripe cherries (few study details given).[4] In another comparison, 15.3% of eggs were laid on unripe cherries, 32.4% on cherries 2 days before harvest and 52.3% on cherries picked at optimal harvest time.[4] In a comparison of different fruits, 20% of eggs were laid on peaches, 7% on plums and 73% on cherries.[4] In a 2004 inspection, 5% of blueberries at the yellow-green stage were damaged by *D. suzukii*, 5% at the early green-pink stage, 16.7% at the mid green-pink stage, 0% at the late green-pink

stage, 21.5% at the blue-green-pink stage and 15% at the fully mature stage.[5] While the results were not analyzed with statistics, *D. suzukii* appeared to oviposit more on ripened cherries and blueberries.

The objectives of the present paper were to study blackberries, blueberries, cherries, grapes, raspberries and strawberries to determine: (1) susceptibility at different ripeness stages for egg laying and development of *D. suzukii*; (2) preference of *D. suzukii* for various cultivars/fruit; (3) the relationship between fruit firmness, pH and sugar content and *D. suzukii* infestation levels.

No-choice tests were used to determine which fruit stage and cultivar are most susceptible on the basis of the physiological capabilities of *D. suzukii*, and choice tests were used to determine preferences of *D. suzukii* on the basis of tactile and

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short-range visual or olfactory cues within 5–10 cm. These controlled laboratory tests will provide a baseline for future studies on fruit preference and *D. suzukii* infestation potential in the field.

2 EXPERIMENTAL METHODS

2.1 Source material

Drosophila suzukii were obtained from a laboratory colony initiated in November 2009 at the USDA-ARS Horticultural Crops Research Unit in Corvallis. Female *D. suzukii* used in experiments were between 5 days old and 2 weeks old with reproductive potential to lay eggs. In Japan, 79 *D. suzukii* females were observed to start ovipositing between 1 day and 4 days and 20 h after pupal emergence with an average of 1 day and 23 h.[6] When possible, fruits were obtained from fields that had received no insecticide treatments (see the footnotes to Table 1). Fruits tested together were often from the same field, or fields within 3–5 km (Table 1). Fruits were stored at 7 °C and used within 10 days, and rinsed in water to remove any residual insecticide. Also, fruits were examined under the microscope for *D. suzukii* eggs, or subsets of the fruits were reared out in the laboratory to make sure that fruits were not pre-infested with *D. suzukii* prior to experimental use.

2.2 No-choice and choice tests

Thirty-four no-choice and choice tests were conducted in the laboratory to determine whether *D. suzukii* would attack fruit at various ripeness stages (26 tests), various cultivars within a given fruit type (seven tests) and various fruit types (one test). Table 1 lists the cultivars and ripeness stages tested under choice or no choice with the number of fruits and *D. suzukii* per cage. While the number of fruits used per cage across no-choice and choice experiments sometimes varied, the ratio of total fruits to female flies was consistent per cage: 1.2 blackberries per female, ∼2.4 blueberries, 1.4 cherries, ∼1.4 raspberries, 0.8 strawberries, 2.4 wine grapes and 7.5 g of fruit per female in the cross-fruit test. In all tests, *D. suzukii* were exposed to fruits presented on the floor of the cage for 24 h at 22 °C, 16 : 8 h light : dark and ∼70% RH. In no-choice tests, one cultivar of a given ripeness stage was exposed to *D. suzukii* in a 22.9 × 22.9 × 25.4 cm white plastic cage with a clear top and sides and a mesh sleeve. In choice tests, all specified treatments were spaced 5–10 cm apart and simultaneously exposed to *D. suzukii*. Choice tests were conducted in the same cages, except the CA blueberry cultivar choice test was conducted in 30.48 cm sided bug dorms (BioQuip, Rancho Domingo, CA). Each of the 34 tests was replicated 6–15 times; treatments were replicated simultaneously on 1–6 test days, and all replications were completed within a 1–20 day period (replications, dates in Table 1).

After 24 h of exposure to *D. suzukii*, fruits were removed, and the number of eggs laid by *D. suzukii* was counted under the microscope for blueberries, cherries and wine grapes. The same blueberries, cherries and wine grapes were transferred to rearing cups with mesh lids kept at room temperature. After 2 weeks, fruits were dissected for developing *D. suzukii* (adults, pupae and larvae). *Drosophila suzukii* eggs are visible on the surface of most fruit skins by viewing the oviposition hole and two white filaments protruding out of the egg, which act as breathing spiracles. Eggs were more difficult to see on blackberries, raspberries and strawberries, which made egg counts unreliable. Also, these three fruits developed extensive mold and juice in the rearing cups, causing some *D. suzukii* to die before 2 weeks. For these reasons, these fruits and all fruits in the cross-fruit test were put into rearing cups after removal from the cage, and the number of developing *D. suzukii* larvae and pupae were counted after 1 week.

For a standard measure of *D. suzukii* susceptibility across the 34 tests using different fruits, the total number of 'eggs laid' or 'developing *D. suzukii*' from one treatment within a cage replicate was divided by the ratio of parental females to the number of treatments in the same cage. This method adjusts data by a relative *D. suzukii* exposure rate for interpreting both no-choice and choice studies at similar scales. No-choice tests always had one treatment per cage, and counts were divided by 5 (= 5 ♀/one treatment). Choice tests had more parental females and 3–12 treatments per cage; without an adjustment for treatment number, the scale of the data would be much smaller than in no-choice studies. For example, each cherry choice cage had 15 females, and the number of eggs laid on 'blush' cherries was divided by 5 and not 15 because 'straw' and 'red' cherries were also present (= 15 ♀/three treatments). The 'percent development' was also calculated (total number of developing *D. suzukii*/total number of eggs laid within a replicate) for blueberry, cherry and wine grapes, but not for blackberry, raspberry and strawberry. Analyses of 'percent development' included fewer replicates when no eggs were laid and were not as robust as the analyses of 'developing *D. suzukii*' counts.

For no-choice tests, a one-way ANOVA tested for the effect of ripeness stage or cultivar type on the number of eggs laid and developing *D. suzukii*, and percent development. For choice tests, a two-way ANOVA was used because treatments in the same cage were not independent, and the cage was a random blocking effect. If needed, log-transformation of count and arcsin transformation of proportional data were used to homogenize the variances. Significant effects of cultivar or ripeness stage ($P < 0.05$) were tested with Tukey's HSD means comparisons. All statistics were analyzed in JMP®7.[7]

2.3 Firmness, pH and brix

The firmness, pH and brix levels (% sugar content) of fruits were measured to determine whether any of these three characteristics were associated with egg laying or development of *D. suzukii*. A subset of fruit of a given cultivar/ripeness was exposed to *D. suzukii* as described earlier, and another subset of 25 fruit of the same cultivar/ripeness was immediately tested for firmness. Firmness was recorded on the FirmTech 2 (BioWorks, Wamego, KS) by the force test option, with all fruits squeezed from 30 to 200 g. A value of 150 g mm^{-1} indicates that 150 g of force will squeeze the fruit 1 mm. Mean firmness of the 25 fruits of a given cultivar and ripeness stage was calculated to represent one data point in a regression analysis (below). Green fruits were too hard and small for measuring firmness, and blackberries, raspberries and overripe blueberries would split during measurements, so no firmness data were taken for these fruits. The same 25 fruits were then measured for pH and brix. Depending on the size of the fruit, each fruit was macerated individually or in groups of 2–5 for an adequate quantity of juice to obtain pH and brix readings. Three pH and three brix readings were taken from the macerated sample, which were averaged per sample. Then an overall mean was taken for a given cultivar and ripeness stage to represent one data point in a regression analysis.

Linear regressions tested the mean firmness, pH or brix value of a given cultivar and ripeness stage in relation to the mean number of eggs or developing *D. suzukii* on the same cultivar and ripeness stage in no-choice and choice studies. A total of 66 or 74 data points were included in the blueberry regressions for firmness and pH/brix respectively, and 43 in cherry regressions.

Table 1. Summary of tests conducted in laboratory cages with fruit exposed to *D. suzukii* (*D. s.*) for 24 h in 2010

Test	No/choice	Comparisons among treatments (number), source of fruit	Rep. (cage)	Number of fruits per cage	♀ ♂ *D. s.* per cage	Dates[k]
Blackberry						
'Marion' ripeness	No choice	Tiny green, green-pink, pink, pink-black, black (5)[a]	7	6	5♀ 4♂	19–20 July
	Choice	Green-pink, pink, pink-black, black (4)[a]	7	3 each, 12 total	10♀ 8♂	20 July
Cultivars	Choice	'Black Diamond', 'Kotata', 'Marion', 'Olallie', 'Silvan', 'Waldo' at black stage (6)[a]	9	3 each, 18 total	15♀ 12♂	22 July
Blueberry	No choice	Pea-green, green, green-pink, pink-blue, blue (5)[a]	7	12	5♀ 4♂	29 June–1 July
'Duke' ripeness	Choice	Green, green-pink, blue (3)[a]	9	8 each, 24 total	10♀ 8♂	30 June
'Earliblue' ripeness	No choice	Pea-green, green, green-pink, pink-blue, blue (5)[b]	7	12	5♀ 4♂	1–6 July
	Choice	Green, green-pink, blue (3)[b]	7	8 each, 24 total	10♀ 8♂	6 July
'Jewel' ripeness	No choice	Pea-green, green, green-pink, pink-blue, blue (5)[d]	7	12	5♀ 4♂	30 May–14 June
	Choice	Pea-green, pink, blue (3)[d]	7	8 each, 24 total	10♀ 8♂	15 June
'Star' ripeness	No choice	Pea-green, green, green-pink, green-red-blue, pink-blue, blue, overripe (7)[d]	7	12	5♀ 4♂	31 May–14 June
	Choice	Pea-green, pink, blue (3)[d]	7	8 each, 24 total	10♀ 8♂	15 June
CA cultivars	No choice	'Duke', 'Earliblue', 'Emerald', 'Jewel', 'Misty', 'O'Neal', 'SantaFe', 'Sharpblue', 'Snowchaser', 'Springhigh', 'Star', 'Wonderful' at blue stage (12)[d,e]	6	12	5♀ 4♂	31 May–7 June
	Choice	''''	9	4 each, 48 total	20♀ 16♂	1–3 June
OR mid-season cultivars	Choice	'Berkeley',[b] 'Bluecrop',[b] 'Bluegold',[c] 'Blueray',[b] 'Duke',[a] 'Earliblue',[b] 'Ivanhoe',[b] 'Patriot',[b] 'Spartan'[b] at blue stage (9)	9	4 each, 36 total	15♀ 12♂	19 July
OR late-season cultivars	Choice	'Aurora',[b] 'Dixi',[b] 'Elliot',[a] 'Jersey',[b] 'Legacy',[c] 'Liberty',[c] 'Ozark Blue'[c] at blue stage (7)	10	4 each, 28 total	12♀ 10♂	5–6 August
Cherry	No choice	Green, straw, blush, red, dark red (5)[f]	6	7	5♀ 4♂	20–26 May
'Bing' ripeness	Choice	Straw, blush, red (3)[f]	6	7 each, 21 total	15♀ 12♂	26 May
'Black Tartarian' ripeness	No choice	Straw, blush, red, dark red (4)[f]	6	7	5♀ 4♂	20–26 May
	Choice	Straw, blush, red (3)[f]	6	7 each, 21 total	15♀ 12♂	24–25 May
'Brooks' ripeness	No choice	Straw, early blush, late blush, pink, early red, red, dark red (7)[g]	6	7	5♀ 4♂	20 April–3 May
	Choice	Straw-early blush, pink-early red, dark red (3)[g]	6	7 each, 21 total	15♀ 12♂	3 May
'Early Burlat' ripeness	No choice	Green, straw, blush, red, dark red (5)[f]	6	7	5♀ 4♂	20–26 May
	Choice	Straw, blush, red (3)[f]	6	7 each, 21 total	15♀ 12♂	24 May
'Tulare' ripeness	No choice	Green, straw, early blush, late blush, pink, red, dark red (7)[g]	6	7	5♀ 4♂	20 April–10 May
	Choice	Green-straw, blush, red (3)[g]	6	7 each, 21 total	15♀ 12♂	4 May

Table 1. (Continued)

Test	No/choice	Comparisons among treatments (number), source of fruit	Rep. (cage)	Number of fruits per cage	♀, ♂ D.s. per cage	Dates[k]
Raspberry	No choice	Tiny, green, green-pink, unripe red, red (5)[a]	7	7	5♀ 4♂	2–6 July
'Coho' ripeness	Choice	Pink-green, green, unripe red, red (4)[a]	7	4 each, 16 total	11♀ 9♂	6 July
Cultivars	Choice	'Cascade Delight', 'Centennial', 'Coho', 'Encore', 'Malahat', 'Willamette' at red stage (6)[a]	9	3 each, 18 total	13♀ 11♂	12 July
Strawberry	No choice	Green-straw, blush, red (3)[a]	7	4	5♀ 4♂	1–3 June
'Hood' ripeness	Choice	Green-straw, blush, red (3)[a]	7	4 each, 12 total	15♀ 12♂	2 June
'Totem' ripeness	No choice	Green-straw, blush, red (3)[a]	7	4	5♀ 4♂	1–3 June
	Choice	Green-straw, blush, red (3)[a]	7	4 each, 12 total	15♀ 12♂	2 June
Wine grape cultivars	Choice	'Chardonnay', 'Merlot', 'Pinot gris', 'Pinot noir' at nearly ripe stage, collected 13 October 2010 (4)[a]	15	6 each, 24 total	10♀ 8♂	13–15 October
Cross-fruit test	Choice	Blackberry,[h] 'Duke' blueberry,[h] cherry,[h] 'Thompson' seedless grape,[h] raspberry,[h] 'Seascape' strawberry (6)	10	~25 g of each fruit[j]	20♀ 16♂	22 July

[a] Research field, Linn Co., OR, no insecticide.
[b] Commercial field, Benton Co., OR, no insecticide.
[c] Commercial field, Linn Co., OR.
[d] Commercial field, Tulare Co., CA.
[e] Research field, UC Kearney Agricultural Center, Parlier, Fresno Co., CA, no insecticide.
[f] Commercial field, San Benito, San Joaquin Co., CA.
[g] Commercial field, Kern Co., CA.
[h] Store purchased, source unknown.
[i] Residence, Benton Co., OR, no insecticide.
[j] 5–7 blackberries, 11–13 blueberries, 2–3 cherries, 3–4 grapes, 8–13 raspberries, 1–3 strawberries.
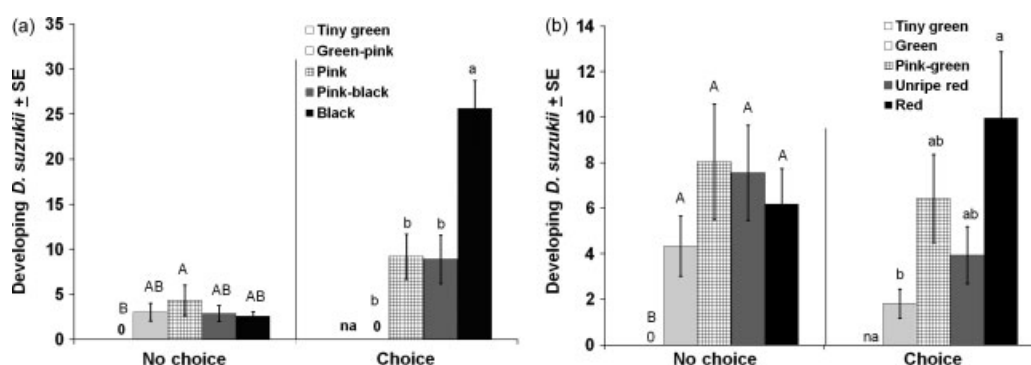[k] Replicates set up on 1–6 days within a 1–20 day range.

Figure 1. Mean number of developing *D. suzukii* from berries of each ripeness stage among (a) 'Marion' blackberries and (b) 'Coho' raspberries, expressed per relative exposure rate to parental females. Letters denote a significant difference by Tukey's HSD, $n = 7$, 'Marion' no-choice $F_{4,30} = 2.6$, $P = 0.053$; 'Marion' choice $F_{3,18} = 17.2$, $P < 0.001$; 'Coho' no-choice $F_{4,30} = 17.7$, $P < 0.001$; 'Coho' choice $F_{3,18} = 3.8$, $P = 0.03$.

Fewer cultivars and ripeness stages of blackberries, raspberries and strawberries were tested, and these regressions included only 12–15 data points.

3 RESULTS AND DISCUSSION

3.1 Blackberry and raspberry (caneberries)

Among 'Marion' blackberries and 'Coho' raspberries in no-choice tests, *D. suzukii* would develop on the four stages of ripeness from green to ripe, but not on the tiny green stage (Figs 1a and b). No significant differences were observed in the number of developing *D. suzukii* between the green to ripe stages, possibly owing to the forcing of flies in a no-choice environment. However, berries are expected to be present as a mix of different ripeness stages in the field, and increased differences were observed between the ripeness stages in choice tests. None to few *D. suzukii* developed on the green stage, intermediate levels developed on the coloring stages and the most developed on the ripe stage (Figs 1a and b).

For cultivar preference trials, about 2.5- and 2.8-fold more *D. suzukii* developed on 'Black Diamond' than on 'Olallie' and 'Silvan' blackberries respectively (Table 2). No differences were observed among the six raspberry cultivars (Table 2). For both caneberries, the mean pH of the berry of a given ripeness stage/cultivar did not change with the number of developing *D. suzukii*, based on a regression with 15 data points (Table 6). However, as the brix levels increased, more *D. suzukii* developed from caneberries (Table 6), confirming an expectation that *D. suzukii* may prefer or develop better on riper and hence sweeter fruit.

3.2 Blueberry

For 'Duke' and 'Earliblue' blueberries in no-choice ripeness tests, few eggs were laid on pea-green and green stages, and very few larval, pupal or adult *D. suzukii* were observed to develop on them at 2 weeks (Table 3). In 'Earliblue' no-choice and 'Duke' choice tests, the percent development was lower on pea-green and green than on ripe stages (Table 3). Among 'Star' and 'Jewel', few eggs were laid on pea-green berries, but about three and ten eggs were laid on green berries respectively (Fig. 2a, Table 3). Yet, percent development on the same green berries was 41% in 'Star' and 23% in 'Jewel', and a lower percent developed on green than on ripe blue 'Jewel' (Fig. 2c, Table 3), suggesting that green blueberries were not highly suitable for development of *D. suzukii*. For each of the four cultivars in choice tests, the ripe blue stage and color changing stage of green-pink or pink-blue were preferred for

egg laying, and development of *D. suzukii* was higher among ripe blue than among the green stage and sometimes the green-pink stage (Table 3, Fig. 2b). Overripe 'Star' had very few flies develop on them, similarly to the pea-green stage (Fig. 2a). These overripe berries dried out in the 2 week period, which may explain why these were not suitable hosts. A similar trend was observed among late-stage 'Napolean' cherries, where ten *D. suzukii* eggs were laid on each fruit and percent emergence was recorded.[4] Only 50% of eggs laid resulted in adult emergence from unripe colored cherries, 90% emerged from cherries 2 days before harvest, 100% emerged from harvested to overripe cherries, but only 10% emerged from spoiled cherries.[4]

Among 12 blueberry cultivars grown in California, there were no observed differences in the number of eggs laid or developing *D. suzukii* in both no-choice and choice tests (Table 3). The percent development was higher on 'Star' than on 'Misty', 'O'Neal' and

Table 2. Mean number of developing *D. suzukii* from blackberry and raspberry in laboratory tests

		Choice
Test	Treatment	Developing *D. suzukii* (mean $\pm$ SE)[a]
Blackberry cultivars	'Bl. Diamond'	20.7 ± 4.55 a
	'Kotata'	9.78 ± 1.58 ab
	'Marion'	15.0 ± 2.67 ab
	'Olallie'	8.36 ± 1.29 b
	'Silvan'	7.42 ± 1.76 b
	'Waldo'	13.4 ± 2.81 ab
	ANOVA	$F_{5,40} = 3.5$
		$P = 0.01$
Raspberry cultivars	'Cascade Delight'	8.21 ± 1.78
	'Centennial'	15.3 ± 4.79
	'Coho'	12.8 ± 3.81
	'Encore'	7.64 ± 2.51
	'Malahat'	11.8 ± 2.76
	'Willamette'	12.5 ± 2.78
	ANOVA	$F_{5,40} = 0.80$
		$P = 0.55$

[a] Counts from one treatment were divided by the number of parental females/the number of treatments present in the same cage replicate; the number of replicates and berries and flies per replicate are given in Table 1; letters denote significance differences by Tukey's HSD.

Table 3. Mean number of eggs laid, developing *D. suzukii* (*D. s.*) and percent development from blueberries of various ripeness stages and cultivars in no-choice and choice laboratory tests

Test	Treatment	Mean ± SE[a]					
		No choice			Choice		
		Eggs laid	Developing *D. s.*	Percent development	Eggs laid	Developing *D. s.*	Percent development
'Duke' ripeness	Pea-green	0.314 ± 0.162 c	0.029 ± 0.029 b	25.4 ± 8.1			
	Green	0.20 ± 0.20 c	0 ± 0 b	0 ± 0	1.77 ± 0.685 b	0.557 ± 0.201 b	29.2 ± 13.0 b
	Green-pink	8.06 ± 1.93 a	2.31 ± 0.597 ab	36.6 ± 6.9	7.90 ± 2.223 a	1.67 ± 0.498 b	18.5 ± 4.5 ab
	Pink-blue	2.49 ± 0.955 bc	0.2 ± 0.115 b	23.9 ± 15.7			
	Blue	6.37 ± 1.55 ab	4.11 ± 1.36 a	49.7 ± 14.7	9.67 ± 2.10 a	6.03 ± 1.56 a	60.1 ± 8.1 a
	ANOVA	$F_{4,30} = 9.0$	$F_{4,30} = 7.5$	$F_{4,20} = 1.8$	$F_{2,16} = 8.1$	$F_{2,16} = 10.2$	$F_{2,16} = 5.7$
		$P < 0.001$	$P < 0.001$	$P = 0.17$	$P = 0.004$	$P = 0.001$	$P = 0.013$
'Earliblue' ripeness	Pea-green	1.06 ± 0.654 b	0.039 ± 0.029 b	3.3 ± 3.3 c			
	Green	0.943 ± 0.282 b	0.20 ± 0.138 b	16.5 ± 10.2 bc	0.943 ± 0.572 b	1.29 ± 1.10	43.6 ± 29.6
	Green-pink	10.0 ± 1.76 a	2.57 ± 0.921 ab	23.0 ± 5.2 bc	6.64 ± 1.73 ab	1.16 ± 0.310	19.5 ± 4.7
	Pink-blue	9.51 ± 1.56 a	3.77 ± 0.635 a	40.5 ± 4.8 ab			
	Blue	5.49 ± 1.11 ab	3.17 ± 0.934 a	54.5 ± 8.1 a	9.56 ± 2.56 a	4.71 ± 1.98	55.1 ± 10.9
	ANOVA	$F_{4,30} = 13.2$	$F_{4,30} = 7.0$	$F_{4,24} = 7.1$	$F_{2,12} = 6.6$	$F_{2,12} = 2.1$	$F_{2,13} = 2.1$
		$P < 0.001$	$P < 0.001$	$P < 0.001$	$P = 0.012$	$P = 0.16$	$P = 0.16$
'Jewel' ripeness	Pea-green	0.943 ± 0.364 b	0.20 ± 0.306 c	14.7 ± 6.5 b	1.07 ± 0.467 b	0.343 ± 0.121 b	50.6 ± 17.0
	Green	10.4 ± 1.82 a	2.51 ± 1.45 ab	22.8 ± 2.5 b			
	Green-pink	8.29 ± 1.88 a	3.57 ± 2.47 ab	37.8 ± 8.2 b			
	Pink-blue	5.57 ± 1.46 a	2.26 ± 1.24 b	39.4 ± 8.2 b	12.0 ± 1.89 a	4.89 ± 0.970 a	43.2 ± 6.6
	Blue	15.0 ± 3.07 a	9.83 ± 4.51 a	67.5 ± 6.5 a	11.1 ± 1.19 a	6.43 ± 0.448 a	61.4 ± 5.9
	ANOVA	$F_{4,30} = 10.1$	$F_{4,30} = 12.4$	$F_{4,28} = 8.5$	$F_{2,12} = 22.3$	$F_{2,12} = 23.7$	$F_{2,12} = 1.1$
		$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P = 0.36$
California blueberry cultivars	'Duke'	11.7 ± 1.83	8.26 ± 4.31	76.4 ± 7.5	11.4 ± 1.23	7.47 ± 1.25	65.6 ± 8.5 ab
	'Earliblue'	7.74 ± 2.30	4.69 ± 1.30	59.0 ± 7.1	12.7 ± 2.37	8.60 ± 1.52	73.0 ± 7.3 ab
	'Emerald'	7.56 ± 2.33	5.48 ± 1.61	68.2 ± 8.8	9.67 ± 2.61	6.13 ± 2.20	72.7 ± 10.1 ab
	'Jewel'	15.0 ± 3.07	9.83 ± 4.51	67.5 ± 6.5	14.9 ± 3.39	9.73 ± 1.76	79.6 ± 12.7 ab
	'Misty'	9.84 ± 1.72	6.4 ± 1.48	74.5 ± 20.1	13.3 ± 2.30	6.0 ± 1.07	47.0 ± 7.3 b
	'O'Neal'	9.93 ± 2.84	5.43 ± 1.33	61.4 ± 12.1	11.8 ± 2.36	6.27 ± 1.20	56.6 ± 7.0 b
	'SantaFe'	9.0 ± 1.99	6.8 ± 2.50	73.6 ± 25.2	12.8 ± 1.48	8.20 ± 1.59	65.4 ± 9.8 ab
	'Sharpblue'	5.7 ± 1.51	3.73 ± 0.93	74.3 ± 8.9	12.3 ± 2.38	9.07 ± 1.62	75.5 ± 7.3 ab
	'Snowchaser'	7.72 ± 2.05	6.72 ± 1.79	87.0 ± 10.7	8.13 ± 2.51	5.53 ± 1.31	75.2 ± 8.0 ab
	'Springhigh'	8.56 ± 2.80	4.88 ± 1.60	59.5 ± 7.3	9.27 ± 1.76	5.40 ± 0.96	65.6 ± 8.7 ab
	'Star'	10.7 ± 2.69	9.06 ± 3.08	78.4 ± 7.7	10.7 ± 2.25	9.20 ± 1.67	93.8 ± 6.4 a
	'Wonderful'	7.12 ± 1.34	5.52 ± 1.29	71.31 ± 9.6	12.7 ± 3.07	6.20 ± 1.36	57.8 ± 7.1 b
	ANOVA	$F_{11,58} = 1.1$	$F_{11,58} = 1.1$	$F_{11,50} = 0.65$	$F_{11,88} = 0.67$	$F_{11,88} = 1.1$	$F_{11,88} = 2.68$
		$P = 0.38$	$P = 0.36$	$P = 0.76$	$P = 0.76$	$P = 0.35$	$P = 0.005$
Oregon mid-season blueberry cultivars	'Berkeley'				8.20 ± 2.25	3.67 ± 1.19	43.9 ± 12.3 b
	'Bluecrop'				8.60 ± 2.11	3.73 ± 0.87	42.5 ± 9.9 b
	'Bluegold'				5.93 ± 1.68	2.73 ± 0.769	46.1 ± 10.9 ab
	'Blueray'				10.9 ± 3.12	4.60 ± 1.15	48.4 ± 10.1 ab
	'Duke'				8.60 ± 2.98	5.20 ± 1.73	66.4 ± 10.7 ab
	'Earliblue'				6.60 ± 1.58	4.13 ± 1.13	61.5 ± 11.4 ab
	'Ivanhoe'				9.87 ± 2.20	5.27 ± 1.48	52.9 ± 13.1 ab
	'Patriot'				5.40 ± 1.80	5.20 ± 1.75	92.3 ± 5.9 a
	'Spartan'				5.80 ± 1.81	3.33 ± 1.01	75.2 ± 11.4 ab
	ANOVA				$F_{8,64} = 0.96$	$F_{8,64} = 0.71$	$F_{8,61} = 2.5$
					$P = 0.48$	$P = 0.70$	$P = 0.021$
Oregon late-season blueberry cultivars	'Aurora'				3.91 ± 0.99	1.28 ± 0.40 b	32.3 ± 22.7 a
	'Dixi'				6.88 ± 2.06	4.67 ± 1.64 ab	65.2 ± 10.8 a
	'Elliot'				4.78 ± 1.23	3.91 ± 0.84 ab	82.0 ± 10.9 a

Table 3. (Continued)

		Mean ± SE[a]					
		No choice			Choice		
Test	Treatment	Eggs laid	Developing *D. s.*	Percent development	Eggs laid	Developing *D. s.*	Percent development
	'Jersey'				5.60 ± 1.29	5.02 ± 1.14 a	94.4 ± 19.1 a
	'Legacy'				4.20 ± 1.19	3.38 ± 0.810 ab	90.7 ± 10.7 a
	'Liberty'				6.77 ± 2.11	1.87 ± 0.995 ab	38.8 ± 20.8 a
	'Ozark Blue'				6.07 ± 1.93	2.22 ± 0.608 ab	69.2 ± 26.3 a
	ANOVA				$F_{6,54} = 0.83$	$F_{6,54} = 2.8$	$F_{6,48} = 2.8$
					$P = 0.55$	$P = 0.019$	$P = 0.020$

[a] Counts from one treatment were divided by the number of parental females/the number of treatments present in the same cage replicate; the number of replicates and berries and flies per replicate are given in Table 1; letters denote significance differences by Tukey's HSD.
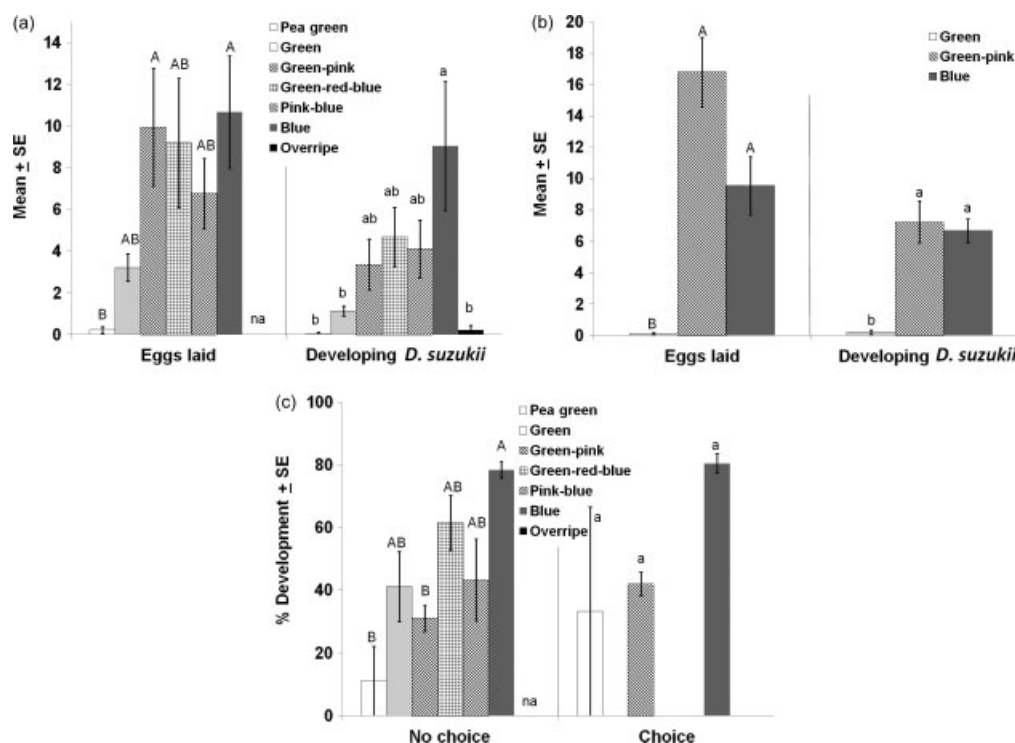

Figure 2. Mean number of eggs laid and developing *D. suzukii* from all 'Star' blueberries in (a) no-choice tests and (b) choice tests, expressed per relative exposure rate to parental females, and (c) percent development. Letters denote a significant difference by Tukey's HSD, $n = 7$, no-choice eggs $F_{5,36} = 3.7$, $P = 0.009$; no-choice developing *D. suzukii* $F_{6,42} = 4.7$, $P < 0.001$; choice eggs $F_{2,12} = 99.5$, $P < 0.001$; choice developing *D. suzukii* $F_{2,12} = 66.3$, $P < 0.001$; no-choice percent development $F_{5,31} = 4.5$, $P = 0.003$; choice percent development $F_{2,10} = 4.3$, $P = 0.045$.

'Wonderful' in the choice test but not the no-choice test (Table 3). Among nine mid-season cultivars grown in Oregon, there were also no differences in eggs or developing *D. suzukii* in choice tests, but the percent development was higher on 'Patriot' than on 'Berkeley' and 'Bluecrop' (Table 3). Among seven late-season cultivars grown in Oregon, there were no differences in eggs laid, but the numbers of developing *D. suzukii* were different between cultivars in choice tests (Table 3). About 3.9-fold more *D. suzukii* developed on 'Jersey' than on 'Aurora'. Further field investigation is needed to determine whether varietal differences are substantial enough to have practical implications.

The firmness, pH and brix recorded from blueberries weakly to moderately correlated with the level of *D. suzukii* infestation (Table 6). As blueberry firmness increased for a given cultivar and ripeness stage, fewer eggs were laid and fewer *D. suzukii* developed from those berries. This follows the expectation that firmer fruit is probably harder for *D. suzukii* to utilize. As pH increased, more eggs were laid and more *D. suzukii* developed, suggesting that this fly may fare better in less acidic blueberries. Similarly to caneberries, as brix increased on blueberries, more eggs were laid and developed.

3.3 Cherry

In no-choice tests with three cherry cultivars that had green stages available for testing, very few or no eggs were laid on green 'Bing', 'Early Burlat' and 'Tulare', and no *D. suzukii* developed on the green stages of 'Bing' and 'Tulare' (Table 4). Egg laying increased on dark-red 'Bing', red 'Black Tartarian' and 'Early Burlat', and on late-blush to dark-red stages of 'Tulare'. For all five cultivars,

Table 4. Mean number of eggs laid, developing *D. suzukii* and percent development from cherries in no- choice and choice laboratory tests

| | | Mean ± SE[a] | | | | | |
| | | No choice | | | | Choice | |
Test	Treatment	Eggs laid	Dev. *D. s.*	Percent development	Eggs laid	Dev. *D. s.*	Percent development
'Bing' ripeness	Green	0.367 ± 0.182 b	0 ± 0	0 ± 0			
	Straw	0.967 ± 0.316 b	0.367 ± 0.216	43.9 ± 18.8	0.533 ± 0.161 b	0.033 ± 0.033 b	16.7 ± 16.7
	Blush	3.87 ± 0.709 b	1.0 ± 0.447	27.9 ± 13.1	4.07 ± 0.801 a	1.77 ± 0.448 a	37.9 ± 8.6
	Red	2.87 ± 0.799 b	0.6 ± 0.163	22.9 ± 8.2	4.10 ± 1.10 a	0.60 ± 0.186 b	24.1 ± 8.4
	Dark red	10.3 ± 1.67 a	1.07 ± 0.472	12.0 ± 4.3			
	ANOVA	$F_{4,25} = 19.4$	$F_{4,25} = 2.0$	$F_{4,22} = 1.64$	$F_{2,10} = 13.0$	$F_{2,10} = 11.8$	$F_{2,10} = 0.74$
		$P < 0.001$	$P = 0.126$	$P = 0.20$	$P = 0.002$	$P = 0.002$	$P = 0.50$
'Black Tartarian' ripeness	Straw	6.0 ± 1.46 ab	5.67 ± 1.24 ab	78.1 ± 12.0 a	4.23 ± 2.55 b	2.87 ± 0.846 b	35.8 ± 6.5
	Blush	3.23 ± 0.802 b	2.20 ± 0.524 ab	72.7 ± 16.9 a	9.20 ± 4.11 ab	2.90 ± 0.409 b	64.8 ± 7.3
	Red	16.77 ± 5.20 a	15.3 ± 6.66 a	78.3 ± 12.1 a	15.77 ± 2.66 a	9.60 ± 1.53 a	62.1 ± 4.3
	Dark red	8.10 ± 1.52 ab	0.167 ± 0.061b	2.7 ± 1.0 b			
	ANOVA	$F_{3,20} = 4.3$	$F_{3,20} = 3.9$	$F_{3,19} = 6.6$	$F_{2,10} = 10.4$	$F_{2,10} = 19.6$	$F_{2,10} = 7.7$
		$P = 0.018$	$P = 0.024$	$P = 0.003$	$P = 0.004$	$P < 0.001$	$P = 0.01$
'Brooks' ripeness	Straw	2.30 ± 1.13	0.867 ± 0.406	28.6 ± 13.1	1.0 ± 0.253 b	0.90 ± 0.252 b	88.3 ± 11.0
	Early blush	2.23 ± 0.79	1.20 ± 0.524	71.4 ± 30.9			
	Late blush	3.70 ± 0.99	1.77 ± 0.676	36.6 ± 9.5			
	Pink	5.60 ± 1.79	1.03 ± 0.307	22.3 ± 4.9	3.40 ± 1.19 ab	1.73 ± 0.657 b	46.8 ± 15.9
	Early red	11.9 ± 4.62	4.67 ± 2.58	32.9 ± 5.0			
	Red	12.1 ± 2.39	4.33 ± 0.555	41.8 ± 9.2			
	Dark red	5.87 ± 1.95	2.23 ± 0.682	46.6 ± 21.5	5.83 ± 0.789 a	3.30 ± 0.546 a	62.6 ± 10.8
	ANOVA	$F_{6,35} = 3.3$	$F_{6,35} = 2.07$	$F_{6,34} = 0.98$	$F_{2,10} = 8.9$	$F_{2,10} = 6.0$	$F_{2,9} = 2.5$
		$P = 0.011$	$P = 0.083$	$P = 0.453$	$P = 0.006$	$P = 0.019$	$P = 0.136$
'Early Burlat' ripeness	Green	0.60 ± 0.278 b	0.30 ± 0.251 c	35.6 ± 22.1 ab			
	Straw	2.87 ± 1.85 b	1.33 ± 0.842 bc	28.1 ± 13.4 ab	4.17 ± 1.80 b	0.90 ± 0.449 b	33.7 ± 11.5
	Blush	5.43 ± 1.09 b	3.40 ± 0.952 ab	62.3 ± 8.9 a	9.03 ± 2.78 a	5.03 ± 1.40 b	57.8 ± 3.0
	Red	12.9 ± 2.21 a	5.33 ± 0.786 a	43.5 ± 6.1 ab	17.9 ± 2.61 a	9.70 ± 1.05 a	55.9 ± 3.9
	Dark red	3.73 ± 2.94 b	0.067 ± 0.067 c	0.83 ± 0.83 b			
	ANOVA	$F_{4,25} = 10.0$	$F_{4,25} = 11.0$	$F_{4,24} = 3.9$	$F_{2,10} = 12.7$	$F_{2,10} = 16.1$	$F_{2,10} = 3.22$
		$P < 0.001$	$P < 0.001$	$P = 0.014$	$P = 0.002$	$P < 0.001$	$P = 0.084$
'Tulare' ripeness	Green	0.50 ± 0.326 b	0 ± 0 b	0 ± 0b			
	Straw	2.50 ± 0.638 ab	0.567 ± 0.381 b	24.4 ± 16.1 ab	1.13 ± 0.50 b	0.50 ± 0.277 b	41.1 ± 16.8
	Early blush	2.70 ± 0.940 ab	0.667 ± 0.161 b	40.4 ± 13.0 ab			
	Late blush	8.57 ± 2.59 a	4.47 ± 1.35 a	51.6 ± 4.8 ab	12.23 ± 7.97 a	7.97 ± 3.0 a	67.8 ± 7.4
	Pink	6.80 ± 1.79 ab	2.87 ± 1.12 ab	35.1 ± 11.2 ab			
	Red	9.73 ± 2.32 a	6.10 ± 1.13 a	65.5 ± 4.5 a	11.17 ± 7.87 a	7.87 ± 3.10 a	56.4 ± 16.3
	Dark red	9.20 ± 1.89 a	2.83 ± 0.791 ab	29.1 ± 3.8 ab			
	ANOVA	$F_{6,35} = 4.9$	$F_{6,35} = 6.9$	$F_{6,29} = 3.06$	$F_{2,10} = 8.1$	$F_{2,10} = 5.3$	$F_{2,10} = 0.57$
		$P = 0.001$	$P < 0.001$	$P = 0.019$	$P = 0.008$	$P = 0.027$	$P = 0.58$

[a] Counts from one treatment were divided by the number of parental females/the number of treatments present in the same cage replicate; the number of replicates and berries and flies per replicate are given in Table 1; letters denote significance differences by Tukey's HSD.

the number of developing *D. suzukii* among ripeness stages was similar to egg laying trends. However, few *D. suzukii* developed on 'Bing' cherries, even though a substantial number of eggs were laid in them. These results may have been an experimental artifact because the tested 'Bing' were observed to rot quicker than the other cherries. Percent development was lower on dark-red 'Black Tartarian' and 'Early Burlat' than on blush/red stages, and was lower on green 'Tulare' than on red (Table 4). In choice tests, *D. suzukii* generally laid fewer eggs and developed less on straw and green-straw stages compared with blush and red stages (Table 4). The firmness, pH and brix of cherries were

observed to correlate weakly with *D. suzukii* infestation (Table 6). As firmness and pH increased, the number of *D. suzukii* eggs laid or developing decreased. Unlike blueberries, this suggests that *D. suzukii* may have a slight preference for more acidic cherries. As expected, as brix increased, more eggs were laid on cherries.

3.4 Strawberry and grapes
In no-choice strawberry tests, significantly more *D. suzukii* developed on blush and red than on green-straw-colored

Table 5. Mean number of eggs laid, developing *D. suzukii* and percent development from strawberries and wine grape tests

| | | Mean ± SE[a] | | | | |
| | | No choice | | Choice | | |
Test	Treatment	Eggs laid	Developing *D. s.*	Eggs laid	Developing *D. s.*	Percent development
'Hood' ripeness	Green-straw		4.0 ± 1.67		2.83 ± 1.52	
	Blush		8.0 ± 2.26		10.0 ± 2.91	
	Red		6.97 ± 1.67		8.49 ± 2.02	
	ANOVA		$F_{2,18} = 1.2$		$F_{2,12} = 2.4$	
			$P = 0.32$		$P = 0.13$	
'Totem' ripeness	Green-straw		2.49 ± 0.122 b		3.06 ± 0.721	
	Blush		7.14 ± 0.271 a		5.23 ± 2.06	
	Red		4.06 ± 0.367 ab		7.91 ± 2.02	
	ANOVA		$F_{2,18} = 3.6$		$F_{2,12} = 1.5$	
			$P = 0.05$		$P = 0.27$	
Wine grape cultivar	'Chardonnay'			0.35 ± 0.17	0.027 ± 0.027	5.0 ± 5.0
	'Merlot'			0.61 ± 0.27	0.16 ± 0.11	9.2 ± 6.0
	'Pinot gris'			0.59 ± 0.20	0	0 ± 0
	'Pinot noir'			0.77 ± 0.19	0	0 ± 0
	ANOVA			$F_{3,42} = 0.68$	$F_{3,42} = 1.9$	$F_{3,24} = 2.2$
				$P = 0.57$	$P = 0.14$	$P = 0.12$

[a] Counts from one treatment were divided by the number of parental females/the number of treatments present in the same cage replicate; the number of replicates and berries and flies per replicate are given in Table 1; letters denote significance differences by Tukey's HSD.

strawberries for 'Totem' but not 'Hood' (Table 5). The same trends appeared in choice tests, although differences were not significant for either cultivar. Although reasons are unknown, the lack of observed differences with strawberries may have been due to their rapid color change. Strawberries were picked from the field at a particular stage and immediately used, but some berries noticeably started to change color the next day when they were retrieved from the cages. The fruit characteristics of strawberries influenced *D. suzukii* development, as observed in regression analyses with 12 data points. As firmness of strawberries increased, there was a moderate trend of fewer *D. suzukii* developing on them (Table 6). As brix increased, more *D. suzukii* developed (Table 6).

In wine grape cultivar choice tests, there were no observed differences in the number of eggs laid and developing *D. suzukii* between 'Chardonnay', 'Merlot', 'Pinot gris' and 'Pinot noir', where mean brix ranged from 17.4 to 19.7% (Table 5). Very few eggs were laid (less than 0.8) on any wine grape cultivar, and 0–9% developed from each of the cultivars (Table 5). Oviposition was observed through the intact skin as well as the junction between the pedicel and grape if it was broken. Similar trends have been observed in no-choice tests with table and wine grapes exposed to *D. suzukii* within plastic cups.[8] In their study, oviposition occurred on intact 'Flame' grapes, and consistently occurred on injured 'Flame', 'Early Campbell', 'Merlot' and 'Riesling'.[8] The thickness of grape skin on these varieties could deter *D. suzukii*; however, 'Pinot noir' is considered thin skinned. Future studies would benefit from measuring skin thickness of fruits in relation to susceptibility to *D. suzukii*.

In a choice test with six different fruits, development of *D. suzukii* on all five fruits was greater than on grape; development on strawberries was also greater than on cherry and blueberry; development on raspberry was greater than on blueberry (Fig. 3).

Because the tested fruits were obtained from different sources, additional tests with fruits grown under similar conditions are needed to validate preference between fruit types. The brix levels of these fruits ranged from 9.6 to 19.4% (Fig. 3). Unexpectedly, the most *D. suzukii* developed on strawberries that had the lowest brix value. When examining trends within each fruit type, more eggs were laid and more *D. suzukii* developed on the same fruits with higher brix values (Table 6). However, the trends across the six fruit types suggests that differences in susceptibility between fruit types may be largely influenced by other factors such as color, odor, texture, firmness and size of fruit (if larger fruit are less likely to desiccate).

4 CONCLUSIONS

In 26 no-choice and choice laboratory tests with various ripeness stages of blackberry, blueberry, cherry, raspberry and strawberry, fruits were susceptible to *D. suzukii* once fruit coloration started. None to few eggs were laid on the green stages, and further development was low on green fruit. Few *D. suzukii* developed on selected grape cultivars (table and wine) and overripe blueberries. In close-range choice tests, *D. suzukii* showed some preference for certain blackberry and late-season blueberry cultivars from Oregon (2–4-fold differences), but no cultivar preference among other blueberry, raspberry and wine grape cultivars. When brix levels increased within each fruit type, more eggs were laid or more *D. suzukii* developed on those blackberries, blueberries, cherries, raspberries and strawberries with weak to moderate trends. When *D. suzukii* were exposed to six fruit types simultaneously in close range, strawberry, raspberry, blackberry, cherry and blueberry were more susceptible than green table grapes. Future laboratory tests should include an artificial diet treatment to control for colony fecundity such that tests done at different times of the year or by other research groups could be interpreted more

Table 6. Linear regressions of fruit firmness, pH or brix values on the number of eggs laid or developing *D. suzukii* in fruits from laboratory tests

| Independent variable	Dependent variable	df	F	P	r^2	Equation
Blackberry						
pH	Dev. *D. s.*	1, 13	0.25	0.627		
Brix	Dev. *D. s.*	1, 13	6.2	0.027	0.270	*D. s.* $= -0.209 + 1.25 \times$ brix
Blueberry						
Firmness	Eggs laid	1, 64	19.0	<0.001	0.217	Eggs $= 12.27 - 0.0149$ *times* firmness
Firmness	Dev. *D.s.*	1, 64	27.0	<0.001	0.285	*D.s.* $= 7.99 - 0.0126 \times$ firmness
pH	Eggs laid	1, 72	23.3	<0.001	0.234	Eggs $= -2.77 + 3.10 \times$ pH
pH	Dev. *D. s.*	1, 72	66.8	<0.001	0.474	*D. s.* $= -5.72 + 2.98 \times$ pH
Brix	Eggs laid	1, 72	7.50	0.008	0.082	Eggs $= 2.58 + 0.419 \times$ brix
Brix	Dev. *D. s.*	1, 72	20.7	<0.001	0.213	*D. s.* $= -1.04 + 0.443 \times$ brix
Cherry						
Firmness	Eggs laid	1, 41	25.6	<0.001	0.37	Eggs $= 11.48 - 0.0147 \times$ firmness
Firmness	Dev. *D. s.*	1, 41	8.94	0.005	0.159	*D. s.* $= 5.45 - 0.007 \times$ firmness
pH	Eggs laid	1, 41	5.57	0.023	0.098	Eggs $= 35.02 - 7.097 \times$ pH
pH	Dev. *D. s.*	1, 41	0.679	0.415		
Brix	Eggs laid	1, 41	4.96	0.031	0.086	Eggs $= 1.68 + 0.353 \times$ brix
Brix	Dev. *D. s.*	1, 41	0.37	0.548		
Raspberry						
pH	Dev. *D. s.*	1, 13	0.18	0.682		
Brix	Dev. *D. s.*	1, 13	14.8	0.002	0.496	*D. s.* $= -15.03 + 2.18 \times$ brix
Strawberry						
Firmness	Dev. *D. s.*	1, 10	9.46	0.012	0.435	*D. s.* $= 13.67 - 0.028 \times$ firmness
PH	Dev. *D. s.*	1, 10	0.032	0.861		
Brix	Dev. *D. s.*	1, 10	11.1	0.008	0.479	*D. s.* $= -20.24 + 3.07 \times$ brix
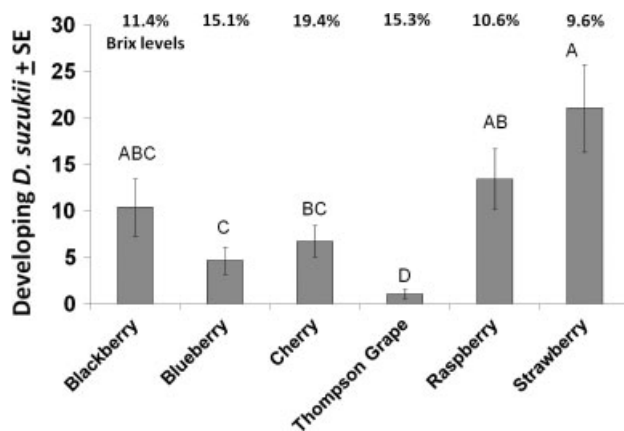
Figure 3. Mean number of developing *D. suzukii* from a choice test with 25 g of each fruit type, expressed per relative exposure rate to parental females. Letters denote a significant difference by Tukey's HSD, $n = 10$, $F_{5,45} = 19.4$, $P < 0.001$.

consistently. Further tests with fruits in the field are needed to evaluate the behavior of flies in their natural habitat in order to provide management guidelines.

ACKNOWLEDGEMENTS

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